ECOLOGY OF TILIA AMERICANA

II. COMPARATIVE STUDIES OF THE FOLIAR TRANSPIRING POWER

JAMES E. CRIBBS

(WITH TEN FIGURES)

A comparative study of the foliar transpiring power of *Tilia* as recorded in the field for dune environments (1) preceded this work, which is an extension of the former investigations, and is concerned with the data recorded for the same species as obtained from a wide range of habitats on clay soils.

The methods employed were essentially the same as described in the former discussion of the dune series. A 3 per cent cobalt chloride standard paper was used in all the work for determining the relative transpiring power, and was applied by means of the clip devised by LIVINGSTON (4). As in the former experiments, readings were taken on two leaves at each station, the same leaves being employed in subsequent readings. Records were taken at approximately hourly intervals, and as recorded represent the average of four to six readings. Curves are plotted for both leaves. The slight difference observed in the readings for the two leaves, which occasionally became considerable, was in most instances attributed to the relative maturity and specialization of the epidermis and cuticle.

Measurements of the chief environmental factors were recorded, and special features of the environment taken into consideration. The chief factors measured were evaporation, relative humidity, atmospheric temperature, soil temperature, wilting coefficient, and growth water. The occurrence of alternate sun and shade, velocity of the wind, fog, and passing thunder showers were special features which were found to bear a definite relation to the oscillating behavior of the transpiration stream. Measurement and computation of these factors were carried out in the same manner as in the preceding experiments.

Nine different stations were chosen, representing the range of habitats frequented by *Tilia* on clay soils. Stations *F*, *G*, and *K* are located on the old Lake Chicago plain, *K* being in Washington Park at Chicago, while *F* and *G* are located in an open forest on the flood plain of the Des Plaines River. These are environments having a strong prairie influence both as to environmental factors and flora composition. Station *H* is located in a mesophytic forest on a glacial upland in western Pennsylvania, where the chief components of the lower flora include such members as *Adiantum*, *Actaea alba*, *Osmorrhiza*, *Botrychium virginianum*, *Aralia quinquefolia*, etc. Station *I* is near *H*, but occupies a position at the edge of an evergreen swamp which lies between glacial moraines. The soil here is of heavy blue clay overlaid by a few inches of rich humus. The undergrowth is composed largely of *Taxus*, *Arisaema*, *Veratrum viride*, and *Symplocarpus*. Station *J* is located at the foot of a steep east-facing embankment at the edge of a creek where the water content of the soil is always high and insulation is low. Station *M* is in a partially wooded rocky ravine where the chief members of the ground flora are *Adiantun*, *Osmunda*, *Arisaema*, etc. Station *N* is near the opening of the same ravine in a more exposed location on alluvial soil washed down from above by the stream. Station *L* is on the flood plain of the Neosho River in Kansas, and represents the species on the western prairie tension line.

This series includes *Tilia* both in its normal environment, the mesophytic forest, and in abnormal ones when considered from an ecological standpoint. It also includes the species near the center of its distribution and on the limits of its range, where it is eliminated by members of another climax series, the prairie. Data have been presented in graph form to better illustrate such correlations as exist between the recorded factors. Graphs for all readings are not presented, because of the recurrence of very similar data at some of the stations. Those recorded, however, represent all the essential facts observed in the work at the various stations.

Normal features of transpiration curve

It has been a commonly observed feature in work on foliar transpiration that the curve representing its index rises quite

rapidly in the morning, beginning at dawn or shortly after. This early rise was attributed by LLOYD (7) to the opening of the

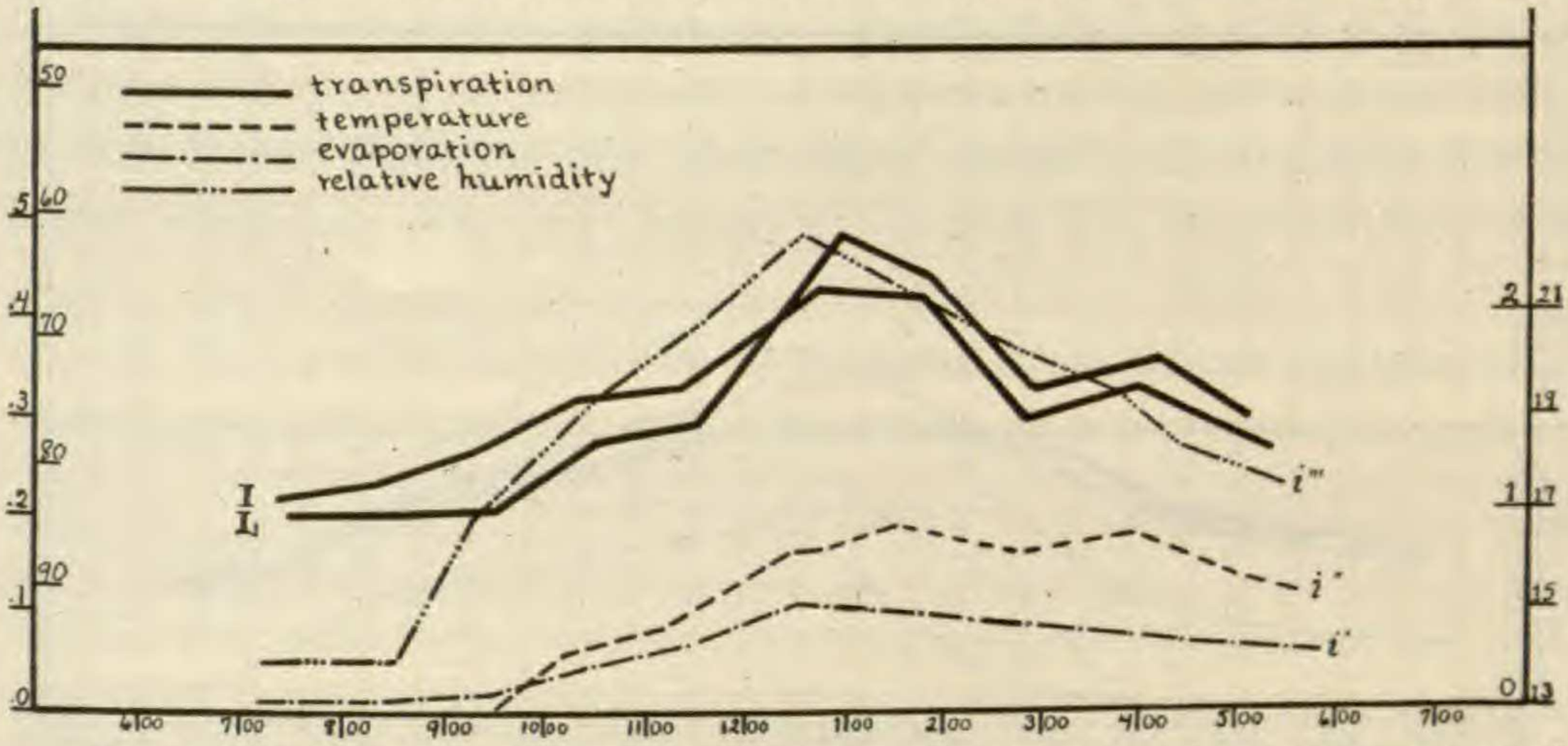

FIG. 1.—Data taken at station *I* on June 7, showing approximate concurrence of maxima in different curves; legend applies to all figures except fig. 7.

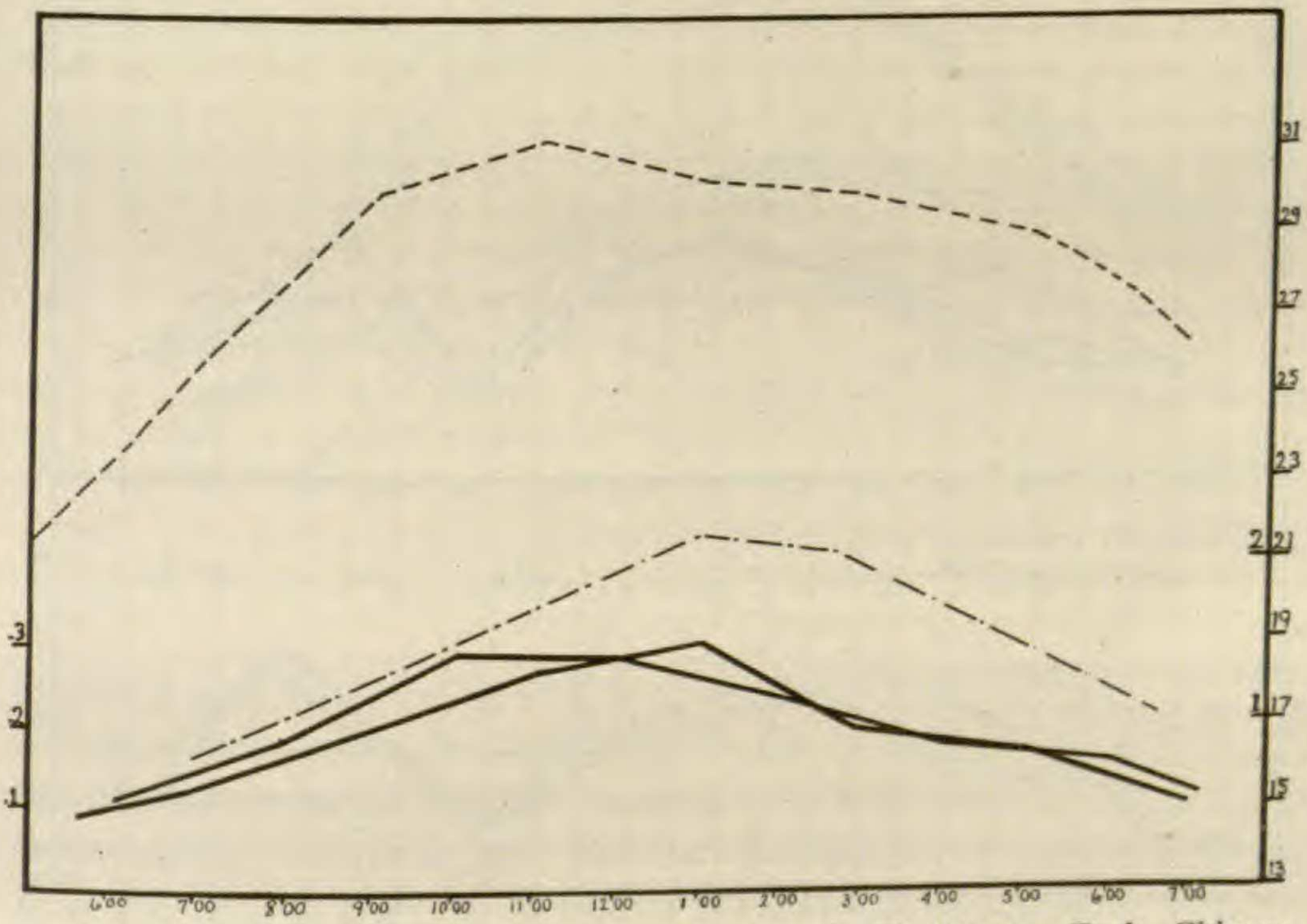

FIG. 2.—Record of data for station *K*, taken in Washington Park, Chicago, August 16; note gradual rise and decline of transpiration curve.

stomata under the influence of light. That there is a sudden opening at this time has been verified by direct examination recently by SAYRE (8). In working on *Nicotiana* and *Verbascum*

he found that the stomata opened rapidly, beginning at about 5:00 A.M. and reaching a maximum about 8:00–9:00 A.M. The study

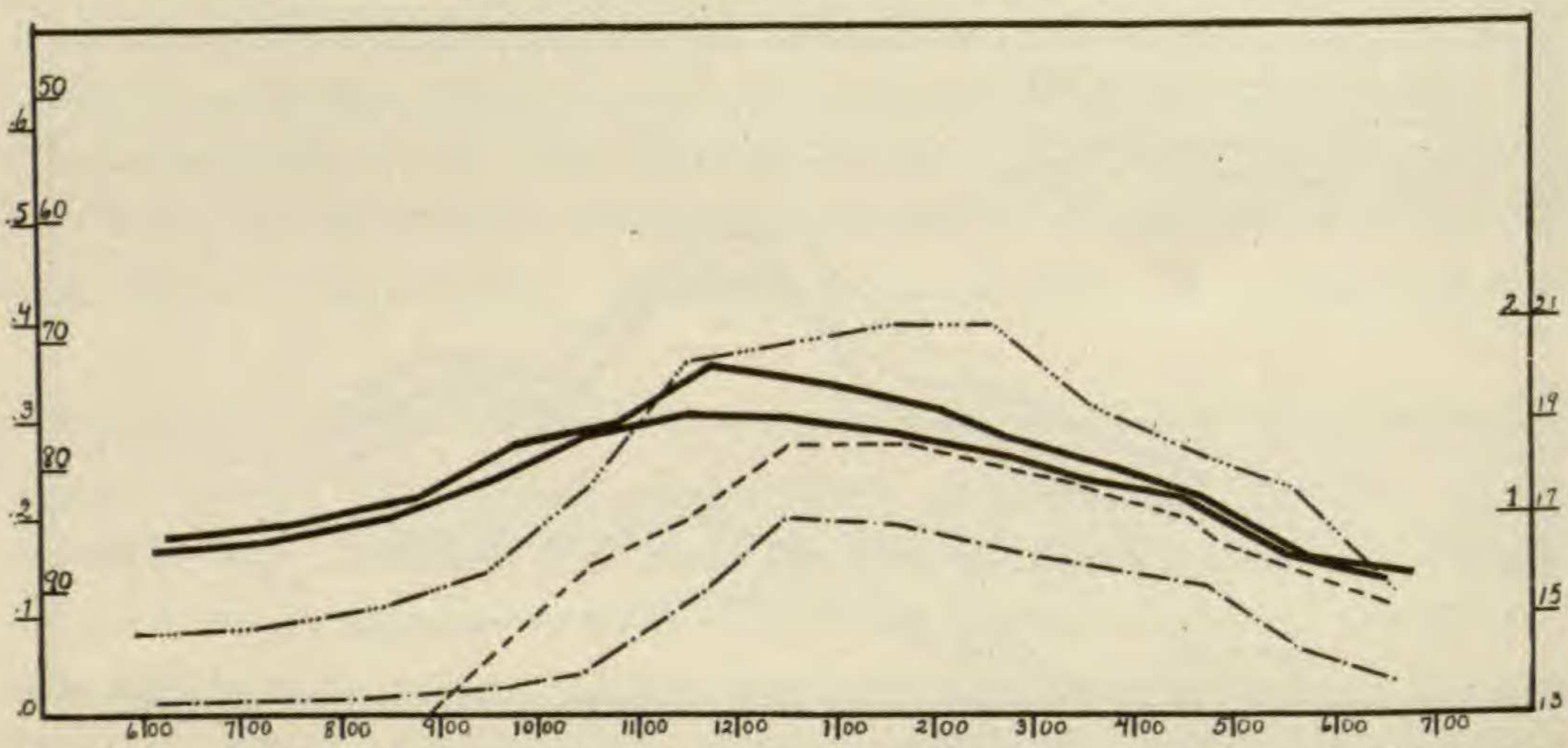

FIG. 3.—Records for station *N*, taken September 2, showing gradual rise and decline in transpiration index, with approximate concurrence of maxima.

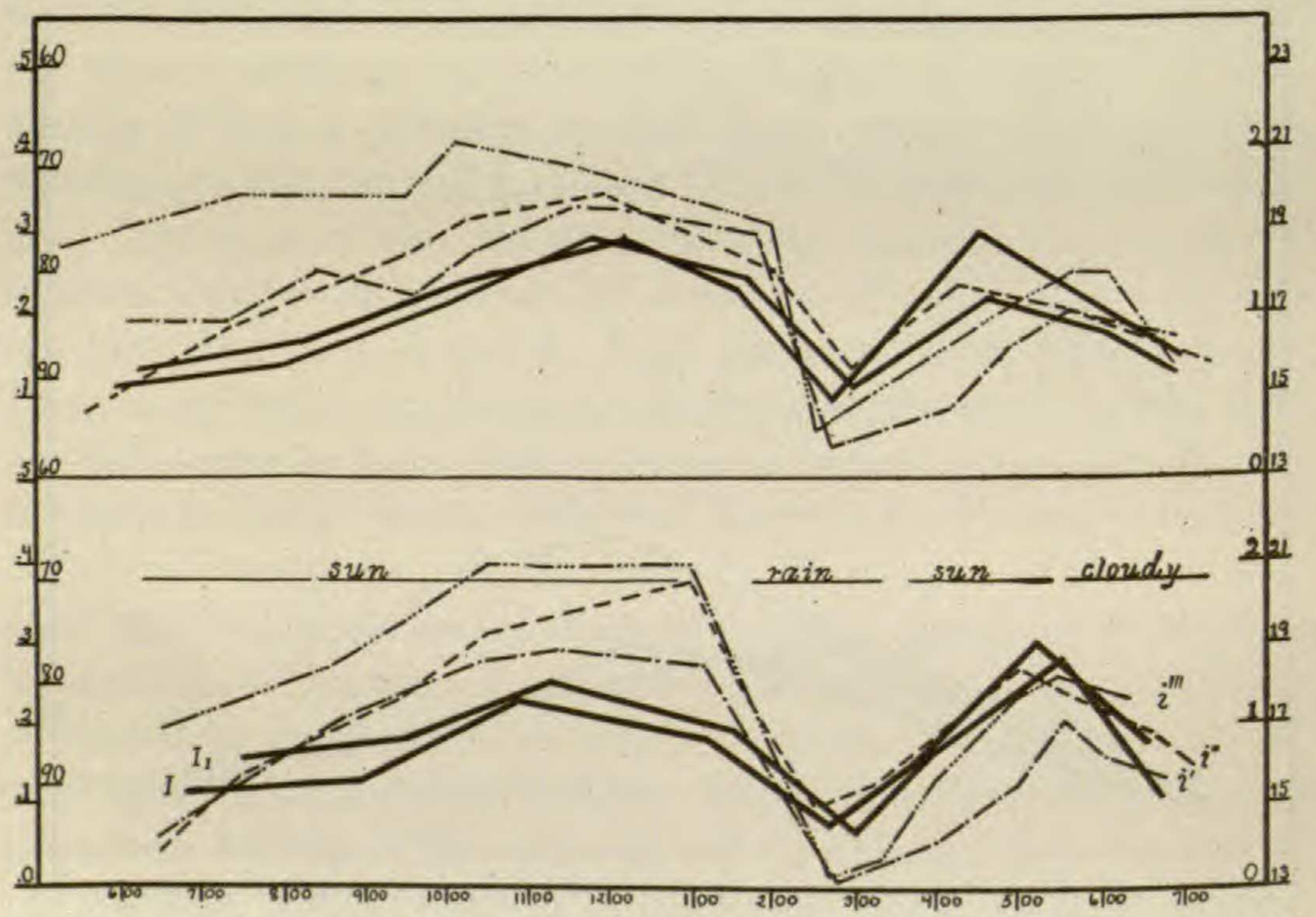

FIG. 4.—Graphs for stations *H* and *I*, taken on June 8, illustrating pronounced depression in transpiration index caused by precipitation; note that both temperature and evaporation curves show like depression and subsequent rise.

of *Tilia* in its more normal habitats on clay has shown a variation from this behavior. Figs. 1, 2, 3, and 4 show that, quite unlike the customary behavior in positions strongly exposed to light, the

transpiration index as recorded in forest habitats more frequently showed a slow steady rise, beginning with the morning opening of the stomata and continuing to a maximum which usually occurred about midday. The maximum was approximately three hours later in the forest than on the open dune sands. It was also much lower relatively than was found to be true for the sand environment. In only one instance was the coefficient observed to reach 0:5 on the forested clay, while in the former case it not infrequently

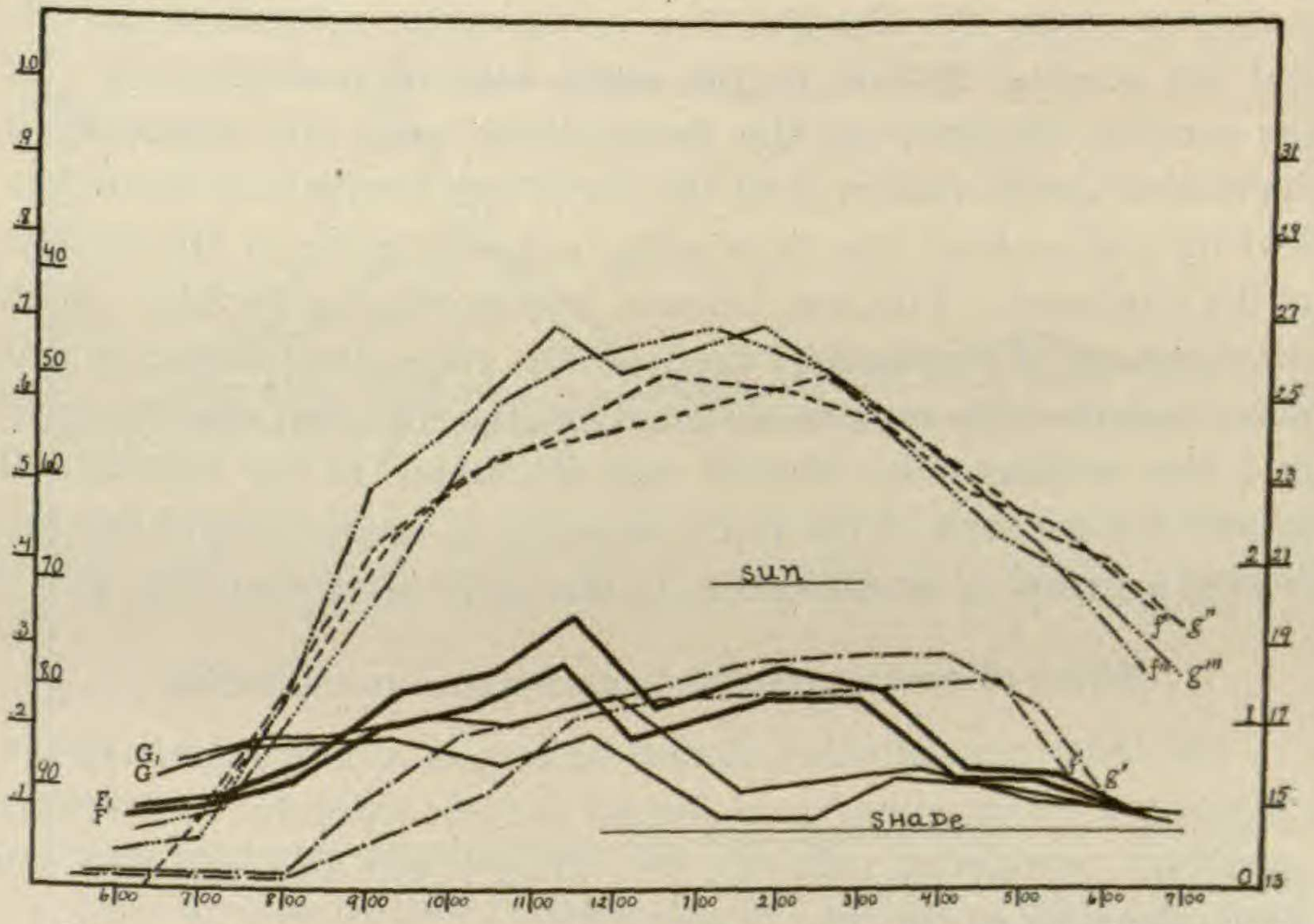

FIG. 5.—Data for stations *F* and *G* in prairie flood plain forest near Chicago; both readings for August 18; stronger saturation deficit recorded for station *G* than for *F*.

attained 0:9. Following the morning maximum, a feature of the transpiration curve, as pointed out by various investigators, is the depression which occurs, causing a divergence from the curves representing temperature, relative humidity, and evaporation. This has been thought to be due to the creation of a deficit of water in the mesophyll cells. Such depressions are strongly evident in the dune graphs, but were inconspicuous throughout the work on *Tilia* in clay habitats. Fig. 5 shows a deficit depression in the graph representing station *G*. It is less evident at station *F* for the same day. Figs. 2 and 3 show a slight divergence from the

evaporation curve, but in all instances the deficit is relatively slight when compared with that recorded in the former studies of this species. The fall of the transpiration curve in the afternoon was just as gradual and slow as the morning rise, by 7:00 P.M. or soon after, reaching approximately the same level as that recorded for 5:00 or 6:00 A.M. preceding the first rise.

The prominent features of the curves as found in this series of studies were a gradual rise, a low maximum which comes approximately at noon, the absence of a conspicuous saturation deficit, and the gradual decline to the night rate of transpiration. In the records obtained on the dunes there was very generally a depression about midday, and the curve was frequently characterized by a secondary rise developing a lower mode in the middle of the afternoon. This was followed by the evening decline. Such development of a secondary mode in the transpiration curves was not a feature of the records obtained on clay soils, but was observed in a few readings only, when it was attributed to the influence of special factors such as the rapid decrease in relative humidity following a period of precipitation in the early afternoon (fig. 4).

Effect of environmental factors upon transpiration

The foliar transpiration stream undergoes various fluctuations, occasioned by the stimulus of certain factors which by temporarily exerting a dominating influence may bring about a pronounced and rapid response in the rate of water loss.

PRECIPITATION.—Passing thunder showers usually caused the coefficient of transpiration to fall very rapidly. Fig. 4 shows the effect of a shower at stations *H* and *I*, these graphs being plotted from data secured on June 8. The general atmospheric conditions other than recorded in the graphs are indicated in the lower figure. It will be seen that at the two stations the same depression appears during the period of precipitation. The corresponding depression in evaporation, temperature, and relative humidity curves shows these factors all working together to produce the same result, namely, a lower transpiration rate. Immediately following the shower, which lasted one and one-half hours, there was a sudden and rapid rise in the transpiration curve, accompanied by a cor-

responding elevation on those of temperature, evaporation, and saturation deficit of the air. The height of the rise was on the whole rather unexpected, inasmuch as the late afternoon was regularly characterized by a steady decline, during which time the stomata were closing. Similar reactions during brief periods of precipitation were recorded during investigation on the dunes, where the depressions were commonly less pronounced.

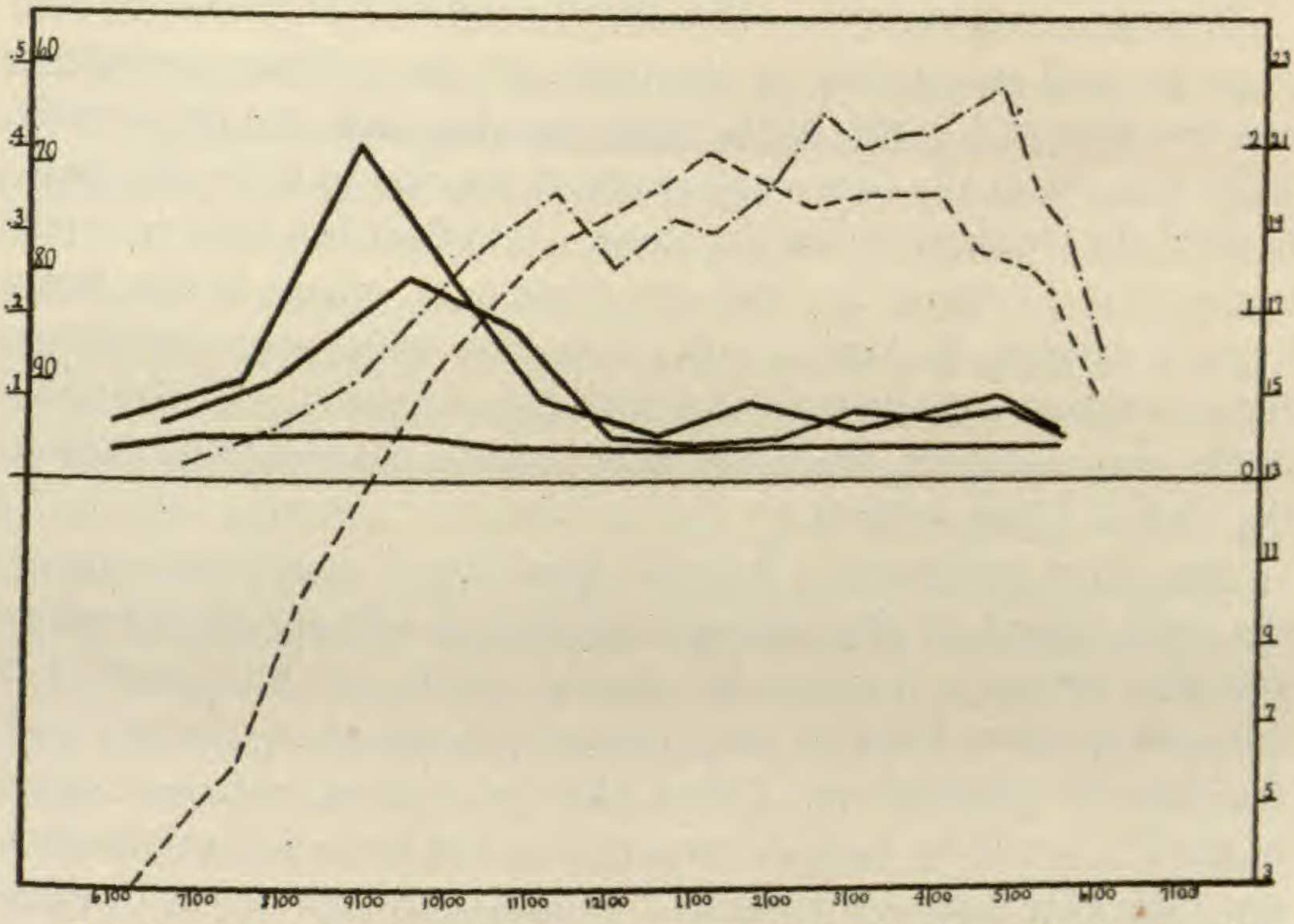

FIG. 6.—Data for station *J*, taken September 3, showing depression in transpiration as result of visible wilting caused by abscission; third solid line represents cuticular transpiration as recorded for adaxial side of leaf; note low temperature in morning.

ABSCISSION.—Fig. 6 shows a curve which is strikingly different from the typical one recorded during this work. It is characterized by a rapid rise to a fairly high maximum which occurred early, about 9:00 A.M. Following the maximum there was a decline, which by midday had almost reached the level of cuticular transpiration. This condition prevailed throughout the remainder of the day, there being a slight and very gradual rise until about 5:00 o'clock. The mesophyll saturation deficit recorded is very conspicuous. This curve is very similar to those described as occurring at stations *A* and *B* on the dunes taken on August 26 (fig. 9, graph 3). In that

instance it was found that the low curve was caused by the soil water being reduced to the wilting coefficient. Such could not be true in this case, however, as the growth water was in excess all the time. The cause of depression at station *J* was found to be associated with abscission. This was likewise an influencing factor in the similar depression formerly referred to, being induced there by the inadequacy of water supply.

WILTING COEFFICIENT.—The effect produced on transpiration when the soil water falls to the point of the wilting coefficient was not observed in any of the work on clay soils, for the growth water content at the time of all readings was found to be adequate to meet the requirements of the plant. Its effect has been referred to, however, in connection with the dune data, where in the dune forest it develops in August. Transpiration under such conditions remains almost entirely cuticular, with the exception of a slight rise in the early morning, when the reserve water accumulated during the night is being utilized.

RELATIVE HUMIDITY.—Relative humidity is considered one of the most potent of the atmospheric factors influencing the transpiration stream. It is the direct cause of the establishment of a diffusion gradient between the internal atmosphere of the leaf and the external atmosphere. Other physical factors initiate change in relative humidity, such as temperature, but because transpiration is a molecular diffusion problem, it should be interpreted as bearing its closest relation to those factors which initiate and directly influence this process. Relative humidity has this close relationship to the foliar water loss, and slight sudden changes in this factor are usually registered in the transpiration curve, even though the porous cup makes no record of it. Reference to fig. 9, graph 2, will illustrate this relation. CURTIS (2), in observing the effect of relative humidity, states that an increase of 8 per cent was followed by a pronounced reduction in the transpiration rate.

EVAPORATION.—The relative humidity and evaporation curves do not always show so close a parallel as might be expected (fig. 9, graph 3), so that in some instances there is greater correlation between those representing temperature and evaporation than between relative humidity and the latter. This divergence is very

largely due to the effect of winds, which, without affecting the humidity, accelerate the loss of water from the porous cup, and may to a less degree affect the transpiration rate. The atmometer shows greater sensitiveness to the influence of wind than does the leaf.

TEMPERATURE.—Temperature exerts a very important influence in the transpiration process by affecting the surface tension films of the mesophyll cells and changing their rate of molecular diffusion. LIVINGSTON (6) has referred to temperature as the probable controlling factor in causing fluctuations in the transpiration stream. An increase in temperature accelerates the diffusion from the mesophyll cells, setting up an increase in the vapor pressure within the leaf. At the same time it also increases the saturation deficit of the external atmosphere, and sets up between the internal and external atmospheres a steeper diffusion gradient, thus leading to a more rapid diffusion of water vapor through the stomata.

Temperature, evaporation, and relative humidity do not explain in full the variation recorded in the foliar transpiring ability of the plant from day to day. Figs. 2 and 5 show transpiration curves typically alike except for a slight depression in the latter at noon. The averages of the relative foliar transpiring power in each of these two cases are almost identical, being 0.198 and 0.193 respectively, yet the atmospheric factors were all exerting the greater physical demand for water at station *K*. Again, if we compare figs. 2 and 3, we find two transpiration curves of the same type, that in fig. 3 being throughout the day approximately 0.05 higher than that at station *K*. Despite this discrepancy the physical factors would call for a transpiration rate considerably lower at station *N* than at station *K*. Moreover, if we compare the graphs represented in figs. 1 and 3, we find that fig. 1 has a higher transpiration rate throughout the afternoon, although the relative humidity is almost the same, and both evaporation and temperature are lower, thus theoretically calling for a lower rate. This failure of the transpiration stream to bear a consistent relationship to the factors of temperature, evaporation, and relative humidity was formerly interpreted as being the influence of stomatal movements, but the fallacy of such interpretation has been pointed out by LLOYD (7) and others. Direct investigation has shown that the stomata open quite early

in the morning, reaching a maximum early (8:00–10:00 A.M.), after which there is a gradual closing until dark, about which time they approximate the closed night condition. During the day it seems that the maximum water loss is always less than the maximum amount which may be diffused from the open stomata, so that the lower general average for certain days must be referred to other causes.

On the sand dunes there is a strong tendency to high transpiration, as is evidenced by the graph representing station *D* for September 2 (1, fig. 8). The evaporation and relative humidity in this instance were closely similar to that recorded for station *N* (fig. 3). The temperature, which registered the greatest degree of difference, averaged about 4 per cent higher, yet the transpiration index was just 100 per cent greater, averaging 0.23 in the latter instance and 0.46 in the former. Thus in any given situation the transpiration may be high or low irrespective of the relative humidity, temperature, and evaporation, although these factors are certainly instrumental in influencing fluctuations in the transpiration stream. In other words, *Tilia* on the open dunes will transpire more actively than the same species in the mesophytic forest, irrespective of atmospheric conditions; and, with similar weather conditions prevailing, in clay environments there may be a considerable variation in the transpiration index from day to day. It is the opinion of the writer that the former of these conditions may be associated with structural differences, and investigations are being made with the hope of giving further light upon this phase of the problem.

GROWTH WATER.—The relation of growth water to the transpiration index has proved interesting. This is the soil moisture content minus the wilting coefficient as expressed by FULLER (3). Fig. 7 illustrates the relation between growth water and transpiration as recorded in the field during the course of investigation. The five stations located on the dune sands are represented by *A*, *B*, *C*, *D*, and *E*. It will be noted that the growth water is very low, ranging from an average of 1.25 to 2.60 per cent. Furthermore, the water loss by transpiration is found to be greatest at the most exposed station, where the growth water average is lowest, and decreases rapidly to a level, which is found at stations *A* and *B*

to be similar to the average rate for the clay positions, where the growth water percentage is relatively high. The average transpiration rate for the mesophytic clays is approximately one-half that exhibited on the open sands. The growth water in the mesophytic forest, despite the lower transpiration rate there, is on the average at least six times as great as on the dunes.

Reference to data for stations located on clay shows that the growth water for these positions fluctuates about 18 per cent,

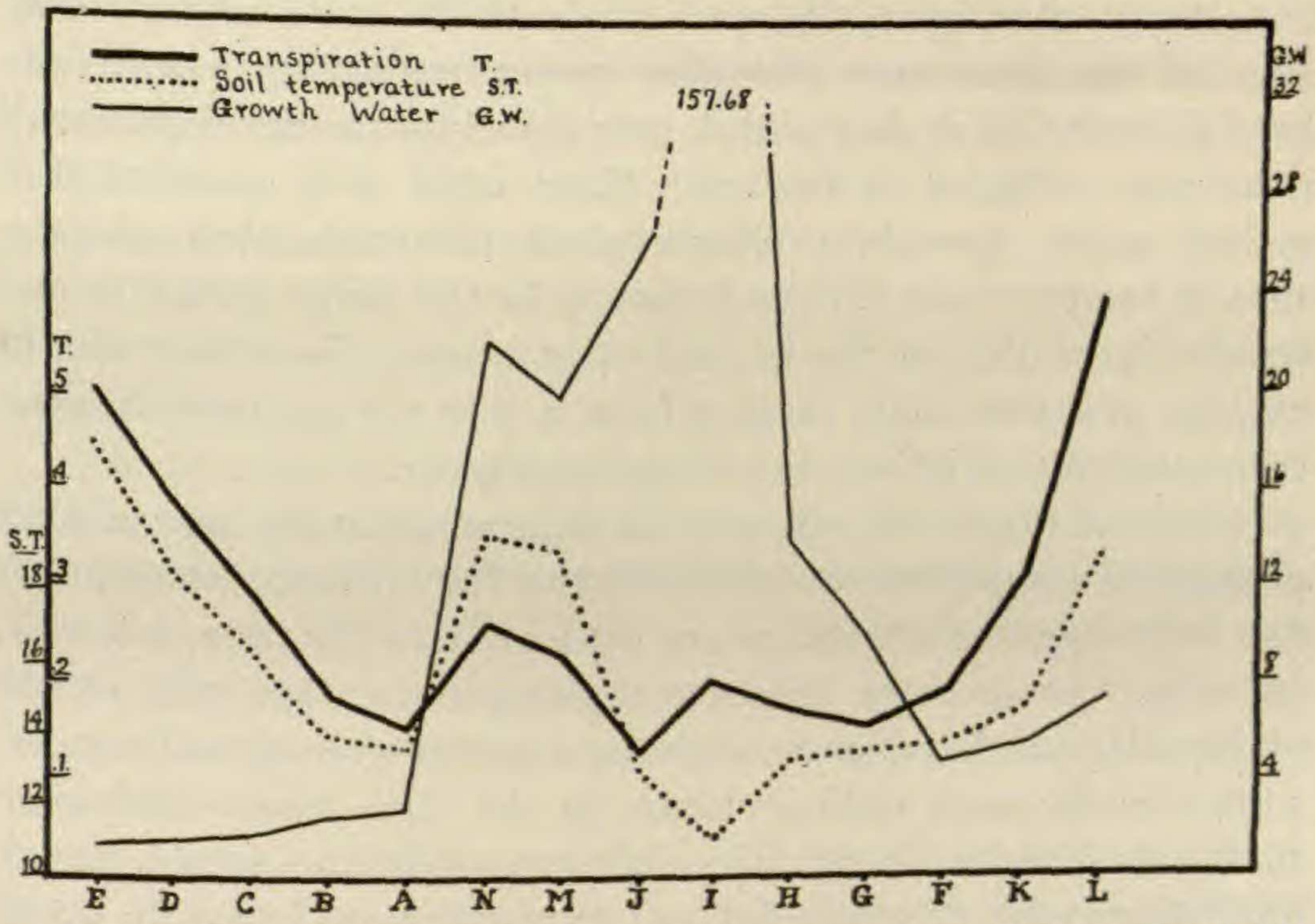

FIG. 7.—Data for soil temperatures, growth water, and transpiration as recorded at all stations on sand and clay; note high transpiration associated with low growth water and high soil temperatures.

being above more often than below this average. Notwithstanding the fact that growth water is always relatively abundant, the transpiring ability is proportionately low, with but two exceptions not exceeding 0.5 at any time during the investigations. The close approximation of the average transpiration rate on the mesophytic clay soils to that of stations *A* and *B* in the dune forest is also evident in fig. 7. Thus the comparative equality in the transpiring power, while the growth water ranges from an average of 2.25 per cent at station *A* to 157.68 per cent at station *I*, strongly indicates

that growth water influences the transpiring ability of the foliage leaves to a less extent than do the atmospheric factors. The only critical evidence of growth water influence during these studies was when it diminished until it approached the wilting coefficient. Visible wilting may then occur, accompanied by a rapid reduction in transpiration until it becomes almost entirely cuticular. Repeated reduction to the wilting coefficient was found to induce early abscission of the leaves, a phenomenon found to take place earlier in the dune forest than upon the open sands of the same region. The effect of abscission upon the foliar transpiring ability has already been shown to be similar to that occasioned by the development of a wilting coefficient in the soil. Thus while it is essential that growth water be available for the plant, there was little evidence that it exerts a conspicuous influence in the daily variation and hourly fluctuation of the transpiration stream, for differences in average available water ranging from 2.5 to 157 per cent show no corresponding variations in transpiring power.

SOIL TEMPERATURE.—It was not determined in the field to what extent soil temperatures influenced the transpiration stream. A few very significant features are evident from the data, however, as when the average foliar transpiring power for each of the stations is considered, and correlated with the average soil temperatures for the same stations, taken on the same days. This comparison is indicated in fig. 7 by the heavy solid and dotted curves, the latter being the curve for soil temperature. It will be noted that the temperature of the soil is high where the transpiration is high and low where the transpiration is low. There was but one instance when a decrease in soil temperature was not accompanied by a corresponding reduction in the transpiration index, this being registered for the swamp habitat. A close parallel was found between average soil temperatures and average transpiration indices.

A second feature is recorded in the relations of growth water and soil temperature. It will be noted that the soil temperature decreases as the growth water increases, so that the lowest soil temperatures are found where the water is most abundant and the highest temperatures where the water is least. The records for

stations *M* and *N* (fig. 7) show a variation from the behavior recorded for the other stations. The readings for these two were taken on one day only, and hence, not being an average of several days' data, are not considered typical. This is especially true as these records were taken in early September during a period of dry hot weather, and hence represent maximum figures for these stations. There is no doubt that the average transpiration and soil temperatures would have been very close to those of station *J* had readings been taken in the late spring and early summer, as was done at the other stations. To what extent this low soil temperature is associated with low transpiring power and high soil temperatures with high transpiring power, cannot be adequately stated at present, but it is known that low soil temperatures produce an inhibiting effect on water absorption by the root system, and would therefore be expected to lead to a lower rate of water loss from the leaf.

The average soil temperature of station *E* is slightly more than double that recorded for station *I*, and the fact that the transpiration index is likewise a little more than doubled is very suggestive. The close parallel recorded between average soil temperatures and average transpiration indices throughout these experiments may be considered evidence that this factor is influential in limiting the foliar water loss.

SUNLIGHT.—Sunlight directly or indirectly produces an effect upon transpiration, inducing a rise in its index. This was pointed out by LIVINGSTON (5) as the result of studies on the effect of light intensities upon the transpiration rate in *Xanthium*, *Physalis*, and *Martynia*. Fig. 6 shows in the morning rise a response to sunlight. The transpiration index in this instance did not show the characteristic response until two hours after daylight, whereas usually the rise begins about dawn. On this day transpiration increased rapidly, beginning when the sunlight fell directly upon the station. The failure to develop an earlier response is attributed to the very low temperature, which was at that time but slightly above the freezing-point. Sunlight falling upon the leaf is followed by the absorption of certain rays which leads to an increase in temperature sufficient to accelerate the diffusion of water from the mesophyll

cells, thus affecting the diffusion gradient and resulting in a greater water loss.

Comparison of swamp and upland mesophytic types

As previously stated, station *H* is located in a typical upland mesophytic forest on mixed morainic clay, and station *I* is located on the border of a swamp where the undergrowth is composed largely of *Taxus* and spring perennials, and where the tree stand

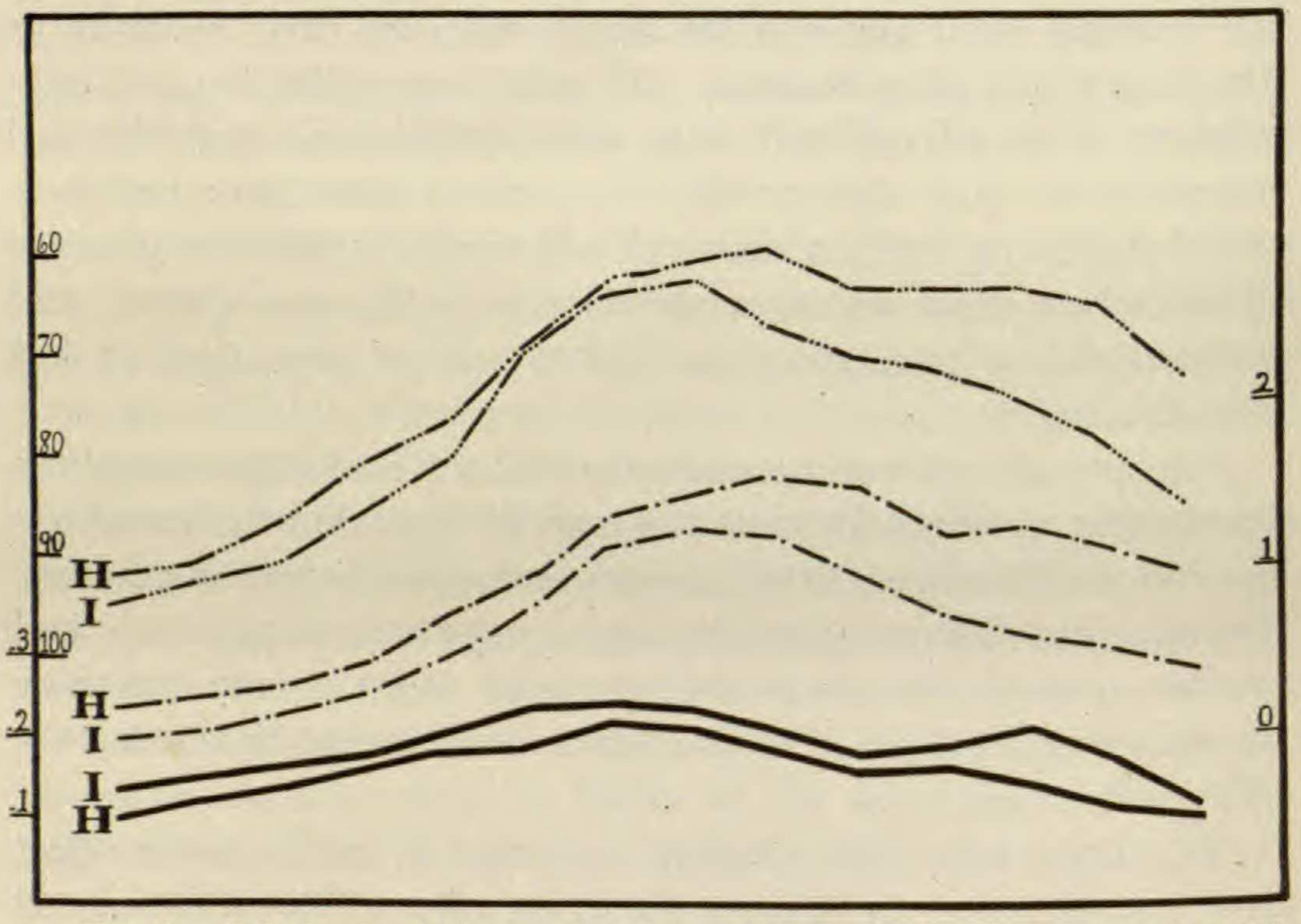

FIG. 8.—Relative humidity, evaporation, and transpiration for stations *H* and *I*, showing average of 5 days' readings at each station.

includes *Tsuga*, *Fraxinus*, and *Acer*. Beneath the humus at station *I* is a heavy blue clay soil which is saturated during practically the entire growing season, and *Tilia*, as do most other forms of vegetation in similar situations, grows to form a low broad hummock, because the roots, being unable to penetrate deeply, spread out on the surface. In this supersaturated environment a peculiar behavior was observed in the transpiration stream. This is shown in fig. 8, which is a composite graph, each curve representing the average of five separate days' readings and including relative humidity, evaporation, and transpiration. It will be noticed that both

relative humidity and evaporation show curves which indicate greater mesophytism at station *I* than at station *H*, but contrary to expectation the transpiration record at the latter is higher throughout the period than in the mesophytic forest. The transpiration curve was higher than that recorded for the much more open forest on the old Lake Chicago bed, where there is a strong prairie influence. Fig. 7 shows that, although the transpiration is relatively high, as on the sand series, the factors of soil temperature and growth water at station *I* are excessive in their extreme opposite relation to the dune condition. Insolation is probably the most influential factor leading to a higher transpiration at this place. It would seem from the relations worked out between transpiration and stomatal aperture by various investigators that the stomata should not prove a limiting factor at the forest station, for the light intensity would seem adequate to insure an opening there which is sufficient to permit a much greater diffusion from the leaves than actually occurs. That increased exposure to light is accompanied by the absorption of light rays by the mesophyll which produce heat and a greater molecular pressure on the water films in the cell walls, and hence leads to a more rapid diffusion of water, seems a reasonable explanation and one which is substantiated by the work of LIVINGSTON (5) on the effect of this factor on transpiration.

Daily variation in transpiring ability

In the former discussion of transpiration on the dunes it was pointed out that if the index of foliar transpiring power were to be utilized in an endeavor to measure the mesophytism of a plant, it should be based on the records of more than a single day, since the variability in the foliar transpiring power is very noticeable from day to day. There is a great daily fluctuation in the transpiring power, just as there is a great hourly fluctuation, and both hourly and diurnal variations are more pronounced on the dunes and prairie than on the forested clays.

Fig. 9 indicates the transpiring ability as recorded at station *C* on the dunes for July 16, 21, and August 26, and it will be observed that on these three days there chanced to be striking differences in the course of the curves representing water loss from the leaves.

The curve for July 16 shows that it is characterized by a late morning rise, a feature quite unusual for the dune series. In addition, the maximum is reached at 1:00 P.M., when the usual occurrence in this environment was a depression at that hour. There was also a high transpiration recorded during the afternoon without the appearance of a secondary mode at 4:00 to 5:00 P.M.

The first of these features, the late morning rise, is attributed to the atmospheric conditions, which show a very low temperature

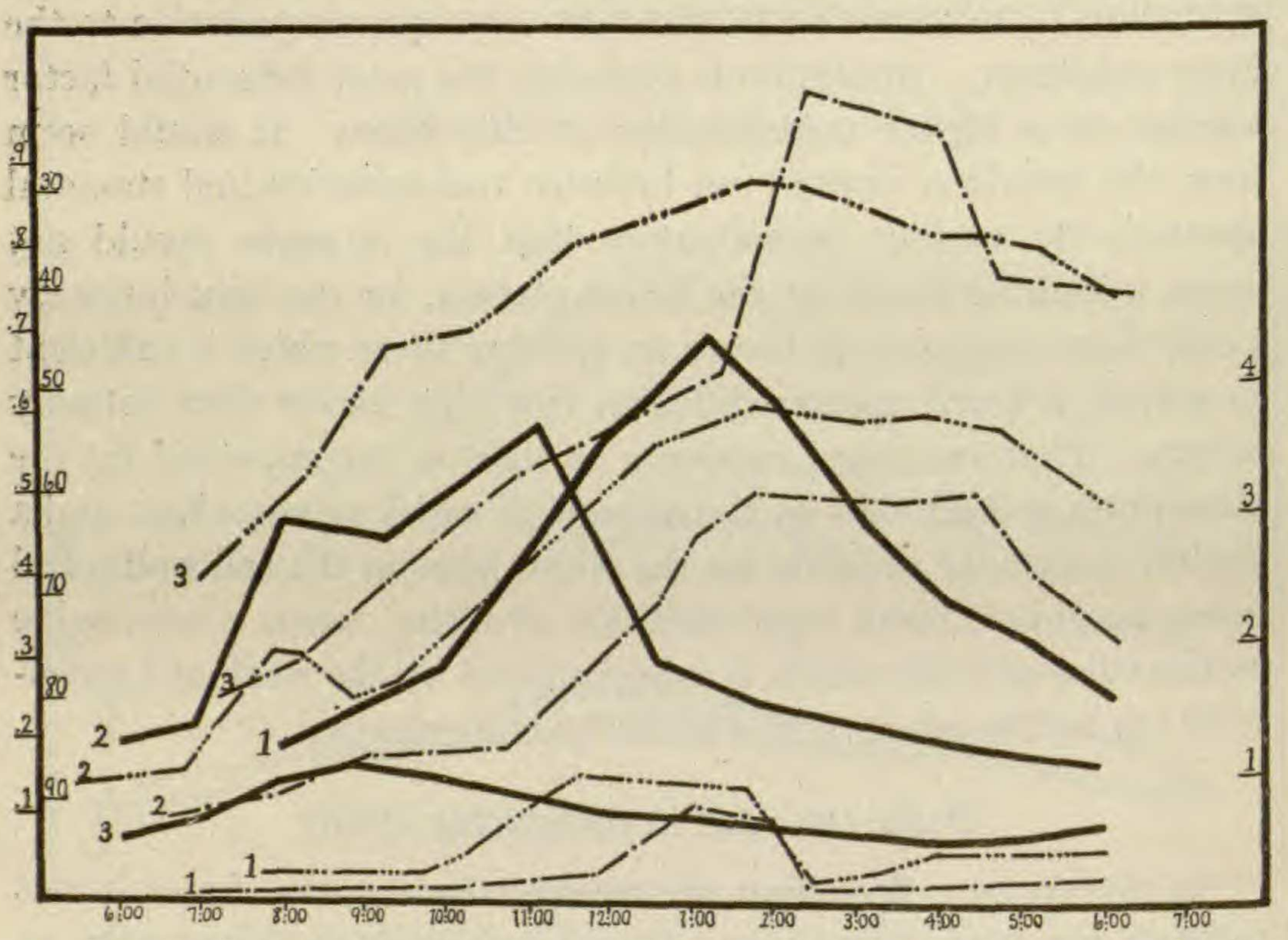

FIG. 9.—Record of readings at station *C* for July 16, 21, and August 26, showing 3 distinct types of curves although records were taken from same leaves.

(about 17°), but especially a low evaporation rate and a high relative humidity. The general weather conditions show a cloudy period, following precipitation from about 5:00 to 6:20 A.M. At 10:00 A.M. the weather became clear, followed by a slight increase in temperature, evaporation, and saturation deficit of the air. Notwithstanding the slow increase in these factors, the foliar transpiration was found to increase much more rapidly in proportion. Thus the maximum transpiration index was greater than was observed to occur under similar conditions on the clays, except

on the prairie, where the factors in general approximate those of the open sands of Lake Michigan, except for the soil type. The high maximum is attributed to the late morning rise and the failure to develop a saturation deficit in the leaves; the factors tending to this end all being impotent throughout the day, namely, high temperature, high evaporation, low relative humidity, high wind velocity, and wide open stomata. A light precipitation in the early afternoon was accompanied by a lowering of temperature and evaporation and an increase in relative humidity to a point approaching saturation, while the transpiration index fell more slowly than was commonly true under such circumstances.

Transpiration curve no. 2 represents the relative foliar water loss for July 21. This curve is characterized by a very early rise because the weather was at that time clear. The rapid ascent was interrupted at 8:00 A.M. owing to the influence of relative humidity. At this time there was a period of cloudiness for an hour or more, when a thunder shower passed just southward without giving precipitation at the station. At 11:00 A.M. the transpiration index had attained its maximum, and conspicuous depreciation between the curves of water loss and evaporation was then developed. There occurred then a period of six hours when the factors for high transpiration increased, but the index nevertheless continued to fall throughout the period. No visible wilting took place on this day, and there appears no evident reason why the transpiration index should not have exceeded that for July 16, judging from the relative humidity, evaporation, and temperature. The difference might be attributed to the less amount of growth water (4.537 per cent) in comparison with that of the latter date (5.910 per cent). I do not believe, however, that the quantity of available water influenced the transpiration very strongly in this instance, for, as already stated, higher indices were regularly attained on the open sands where the growth water was as low as 1.25 per cent. It would seem that the depression takes place at the time the reserve water, accumulated during the night, and held by the translocating system and leaves, plus that continually being added by absorption from the root system, is equalized by diffusion from the leaf. If the water content of the soil is not a limiting

factor, the ability to absorb and translocate very probably becomes so. This would then be a typical "saturation deficit." If this be true, then the maximum to be very high will evidently occur after a very rapid rise, while a less rapid but prevailingly high transpiration rate will utilize the reserve water and reach the limit entailed by anatomical features without having so high an index. There is evidence for support of this in the two curves in question; the average of the indices for the first six hourly readings for July 21 being 0.396, while the average for July 16, computed from the same leaves, for the first six hours preceding the maximum is 0.391, which means that the water loss from a unit area from the first rise in the morning until the attainment of the maximum was practically the same. Granting that the translocating ability limits the maximum rate of transpiration, then, since we are considering data calculated from the same individual with an interval of but five days, we would expect the water loss up to the time of incipient drying to be approximately the same, when the time periods are the same. We may further assume that the water reserve will be quite constant for the same individual on consecutive days when the growth water is adequate to meet all the needs of the plant, for this will be dependent upon the structural features of the plant, which remain quite constant. A slight variation in the reserve would follow a variation in food storage, which is a fluctuating factor, and slight differences in the total transpiration up to the time of the deficit depression will result from different absorption rates which fluctuate with soil temperature. If the transpiration index is high in the morning, the maximum transpiring power will of necessity appear early, for the reserve is utilized rapidly. If the rate is low in the morning, the maximum, if it is attained, will occur relatively late. The maximum transpiring ability is limited by the rapidity of rise in the index and the translocation-absorption ability. The maximum translocation doubtless occurs when the protoplasmic condensation within the mesophyll of the leaf is greatest, since at that time the osmotic pressure within the cells is highest, and the cells will exhibit their greatest affinity for water. This occurs two or three hours after the maximum transpiration. The relatively high transpiration index preceding

the attainment of maximum absorption is possible because of the reserve water which is available in excess of that supplied by the translocation stream.

Curve no. 3, which indicates the transpiration for August 26, shows some features conspicuously unlike those recorded for the two preceding readings. The maximum is lower in this instance than was the minimum index for either of the preceding days. The low amount of growth water, which was only 0.480 per cent at 2.5 dm., was a prominent cause for the lower transpiring power. At 10:00 A.M. visible wilting occurred, and turgidity was not restored within the mesophyll cells of the leaves until about 5:00 P.M. The development of absciss tissue may be considered as contributing to the reduced rate, being earlier at this station than on the open sand, owing to the more frequent production of a wilting coefficient. Evaporation and relative humidity show curves which lie much higher than do those of July 16 and 21. The extremely high evaporation from about 1:30 to 4:30 P.M. was due to high wind velocity.

It will be seen that on different days readings from the same leaves may give widely different results. The three days' readings shown in this instance present different combinations of potent factors, one being a cloudy day with plenty of available water, one a clear day with sufficient growth water, and the third a clear day with low humidity and soil water reduced to the wilting coefficient. Thus the environmental factors which initiate variation in the daily transpiration rate at any given station were found to be the same as those which led to different averages for the various stations. This daily variation is more marked on the sand series than on the clays, although the same phenomena were characteristic of the latter situations. There was found to be more variation in transpiring power between cloudy and clear days than was registered for days when the atmospheric conditions were similar, whether cloudy or clear.

Transpiration on prairie

The transpiration index as recorded for *Tilia* on the prairie indicates that there the species is subjected to a physiological stress in most respects very similar to that found on the dunes (fig. 10).

There is the same tendency on the prairie toward an early rapid rise in the index, and for a maximum which occurs from one to two hours earlier than is characteristic of *Tilia* at the other stations on clay soils. The maximum is relatively very high on the prairie, and is followed quite regularly by a saturation deficit which is more pronounced than that recorded for any other habitat except upon the open dune complex.

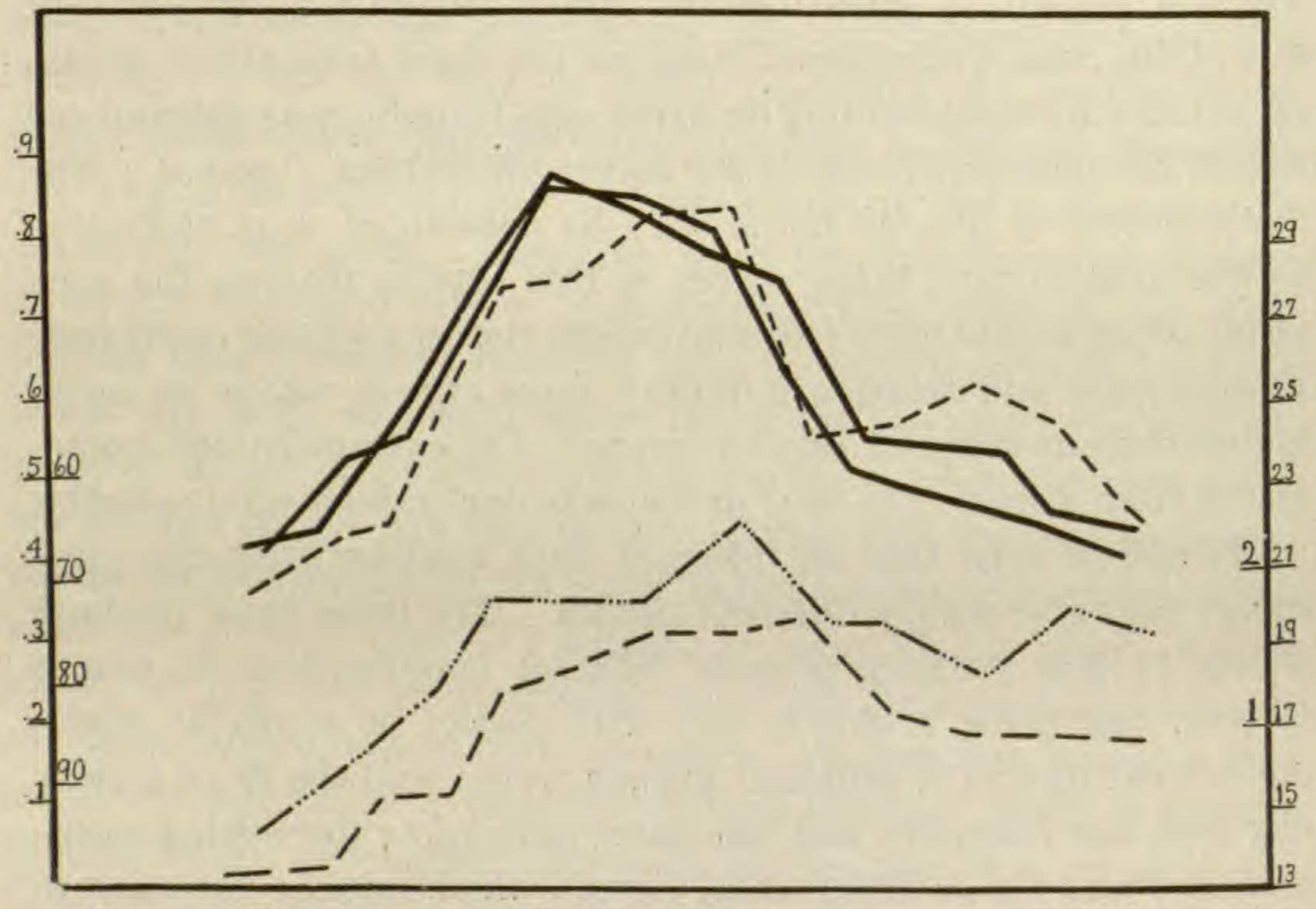

FIG. 10.—Data for station *L* for September 6; note exceptionally high transpiration index characteristic of prairie tension zone; transpiration is great although relative humidity is high and evaporation low.

The prevailing environmental factors show a close similarity to those of the open sands. The growth water is low during much of the summer, the insolation is correspondingly high, the influence of winds is strong and quite constant, prevailing temperatures are higher and are associated with a relative humidity which is low (fig. 10). Thus the features of these two types of associations show remarkable similarity, with the exception of the soil composition and growth water. The growth water falls rapidly during the months of August and September and approaches the dune condition. These factors in conjunction exert an influence which

leads to a high transpiration rate and to the development of morphological features in the leaves which are very similar to those recorded at station *E* on the dunes.

Transpiration in relation to mesophytism

Water content of the soil has long been recognized as a factor which directly influences the climax type of flora that may develop in any given region. The relatively high content as shown for the mesophytic forest has quite generally been ascribed as the reason for the development of the larger thin type of leaf characteristic of that region, in contrast with the smaller more thickened type characterizing open associations. Correlated with this concept frequently has been the idea that transpiration in the mesophytic forest is very high. Observations on the foliar transpiring power of *Tilia* throughout its range of habitats, from the most to the least mesophytic conditions under which it develops, have led to a conclusion in regard to this species which is quite different from that just stated. The greatest transpiring ability was exhibited in the most open situations where the available growth water was least, and the transpiring ability was found to be least in the dense shade of the mesophytic forest and moist ravines where the growth water was relatively very high. It may be asked why the water loss is less in the forest. The question is answered by pointing out that the environmental factors for high transpiration are less potent in the forest than in more exposed positions. Relative humidity is greater, evaporation is less, temperature is lower, light is less intense, soil temperature is lower, and winds are less effective. All of these physical factors combine to give a lower rate of transpiration than occurs in the exposed open situations.

Summary and conclusions

1. The morning rise in the foliar transpiration index for *Tilia* is commonly much slower for the clay series of environments than for the sand dunes, and the maximum attained is comparatively much lower.

2. The time of maximum transpiration is usually from 12:00 to 1:00 P.M. on clay soils, whereas on the sands it occurred from 9:00

to 10:00 A.M. This difference is ascribed to the more rapid utilization of the reserve water which is stored up in the leaves and translocating system of the plant during the night. Thus on the dunes, where the reserve is utilized more rapidly than it is restored by absorption and translocation, there will occur a depression in the index later in the day. On the clay soils, the rise being slower, frequently the reserve is not utilized until midday; hence there occurs a lower maximum and a much less noticeable saturation deficit, or none at all. This means that the maxima of temperature, relative humidity, and evaporation concur in time or more nearly approximate doing so than for the dune series. The closest approximation to this concurrence on the sands was recorded for cloudy days with low temperature and evaporation and a high relative humidity. All these conditions of environment are tendencies toward the prevailing condition in the forest, in contrast with those characterizing open dune situations.

3. The transpiration stream shows a simple curve for readings taken on forested clays, rising gradually to a maximum at noon and falling at approximately the same rate to the night level.

4. The effect of thunder showers is recorded in a sharp reduction in the transpiration index. Frequently when the precipitation occurs in the early afternoon there is a second rise in the transpiration curve to a level in excess of the normal rate for that time, probably owing to the accumulation of a slight reserve, while the transpiration rate is lower than that of absorption.

5. Partial abscission produces an effect not unlike that found accompanying the development of a wilting coefficient. Under these circumstances there is a low morning rise which quite early reaches a maximum, and is followed by a rapid decline accompanied by the closure of stomata and visible wilting, the transpiration falling until it becomes almost entirely cuticular. The morning rise takes place in this instance because of the slight water reserve accumulated during the night.

6. A wilting coefficient did not develop in any of the clay soils, and there was always a considerable amount of growth water available, but its occurrence on the sand series produced an effect closely similar to that occasioned by abscission.

7. Sunlight affects the transpiration stream through its influence in initiating stomatal movements, and has particular reference to the morning rise. Direct sunlight accelerates the water loss, due apparently to a rise in temperature of the mesophyll cells which would be followed by a greater molecular diffusion of water from the cell walls into the lacunae of the leaf, thus increasing the diffusion gradient.

8. Relative humidity is a very potent factor in influencing the transpiration index. By increasing or decreasing, it affects directly the diffusion gradient between the external and internal atmospheres. Sudden changes in this factor almost invariably affected the transpiration stream, even when the atmometer failed to register it. When the relative humidity is great there seldom is any saturation deficit developed, but when it is low and the evaporation rate increases greatly the reserve will probably be consumed and a saturation deficit will follow. Relative humidity is considered a very potent factor leading to such depression in the curve.

9. Growth water exerted less influence in modifying the transpiration rate than did most of the atmospheric factors. There is little evidence that it is a potent factor at all on the clay series. Its direct effect is most noticeable when it approximates the wilting coefficient as was recorded on the sand dunes, when the index is observed to fall rapidly. The growth water was always more than could be utilized in the clay environments, and hence never proved a limiting factor.

10. The part played by soil temperature in maintaining the transpiration stream is considered more important than has generally been ascribed to this factor. The close parallel of the soil temperature and transpiration curves is strongly indicative of its influence (fig. 7), and especially is this significant since there is strong evidence that the absorption rate often becomes a limiting factor. I believe that since soil temperature bears a direct relation to absorption it will eventually be found to be of great significance in limiting the foliar transpiring ability.

11. The highest average transpiring power recorded for the clays, with the exception of the prairie data, was that registered for the swamp habitat. In this environment *Tilia*, while producing

a relatively high water loss as on the dunes, is growing in the very opposite environment in reference to its physical factors. The growth water and relative humidity are greater here than at any other station, while soil temperature, evaporation, and atmospheric temperature are lowest. Of these factors, measured soil moisture might be cited as the causal factor leading to increased transpiration, but it seems improbable that this factor can be responsible for the higher water loss. It is more probably associated with structural features, the correlation of root and leaf development, or the greater exposure to light.

12. The variation in average transpiring power from day to day as recorded for the same leaves is greater for the mesophytic forest than is the difference between the average rates for the most mesophytic and most xerophytic stations, if we consider the clay series only and disregard the prairie record. The converse is true for the dune series.

13. Daily variations in the transpiration stream are most pronounced in the xerophytic situations, and least so in the strongly mesophytic ones.

14. The average transpiring power is less in deep forests and moist ravines than in open woodlands, and less in open forests than in exposed positions on clay. The greatest transpiring ability was recorded on the open sands where there was no humus, and on the prairie.

15. The transpiration curve characteristic of the prairie station is closely similar in its essential features to the curves representing the open dune sands. There is a more rapid morning rise as compared with the forest, owing to the greater light exposure at that period, a tendency to an earlier maximum due to a greater water reserve, a more frequent recurrence of a saturation deficit, and finally a steeper afternoon decline than is commonly recorded for the clay environments.

16. The highest transpiration rates are found to be associated with a low growth water, which is not interpreted as being in any way causal, but as evidence that growth water is of relatively little significance so far as transpiration is concerned until it approaches the wilting coefficient.

17. High mesophytism leads to low transpiration in *Tilia*, and large leaves of thin texture transpire at slower rates than do smaller leaves which are more leathery and resistant in nature.

DRURY COLLEGE
SPRINGFIELD, MO.

LITERATURE CITED

1. CRIBBS, J. E., Ecology of *Tilia americana*. I. Comparative studies of the foliar transpiring power. BOT. GAZ. **68**:262–286. 1919.
2. CURTIS, C. C., Some observations on transpiration. Bull. Torr. Bot. Club **29**:360–373. 1902.
3. FULLER, G. D., Evaporation and soil moisture in relation to the succession of plant associations. BOT. GAZ. **58**:193–234. 1914.
4. LIVINGSTON, B. E., The resistance offered by leaves to transpiration water loss. Plant World **16**:1–35. 1913.
5. ———, Light intensity and transpiration. BOT. GAZ. **52**:417–438. 1911.
6. LIVINGSTON, B. E., and BROWN, W. H., Relation of the daily march of transpiration to the variation of the water content of foliage leaves. BOT. GAZ. **53**:309–330. 1912.
7. LLOYD, F. E., The physiology of stomata. Carnegie Inst. Wash. Publ. no. 82. 1908.
8. SAYRE, J. D., Factors controlling variations in the rate of transpiration. Ohio Jour. Sci. **19**:491–509. 1919.